



Factors influencing cannibalism in the plainfin midshipman fish



Aneesh P. H. Bose*, Karen M. Cogliati, Holly S. Howe, Sigal Balshine

Aquatic Behavioural Ecology Laboratory, Department of Psychology, Neuroscience, and Behaviour, McMaster University, Hamilton, ON, Canada

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Cannibalism of young is a common yet seemingly paradoxical phenomenon observed across a wide variety of taxa. Understanding this behaviour in the context of parental care remains a challenge for evolutionary biologists. A common adaptive explanation for the consumption of offspring is that it serves to increase the current or future reproductive success or survival of the cannibalistic parent by replenishing energy stores and facilitating continued care for any remaining young. Another explanation is that cannibalism may be a competitive response to cuckoldry or lowered certainty of parentage. We tested these ideas using the plainfin midshipman fish, *Porichthys notatus*, a species with an extended period of male-only parental care and documented offspring cannibalism. We found that the occurrence of cannibalism was not linked to the deterioration of body condition, but instead was most frequent during periods of high intrasexual competition and nest take-overs. Our results suggest that cannibalism is not driven by the energetic demands of parental care, but instead by competition among males for nests and females, and the resulting low paternity stemming from both nest take-overs and cuckoldry.

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Cannibalistic behaviour has been observed in a vast range of taxa throughout the animal kingdom (Elgar & Crespi, 1992; Polis, 1981; Smith & Reay, 1991; Soulsby, 2013). Predation upon conspecific offspring has been widely documented across species, even for those that provide a high degree of parental care (Elgar & Crespi, 1992; Polis, 1981). In most caregiving species, parents invest considerable time and resources into offspring production, protection and growth, so cannibalism of offspring appears counter-productive to the goals of a caregiving parent. Evolutionary theory suggests that even with filial cannibalism, the acute loss of current reproductive success associated with the consumption of one's own offspring can be offset by future fitness benefits to the cannibal (Elgar & Crespi, 1992; Manica, 2002; Polis, 1981; Rohwer, 1978; Smith & Reay, 1991). For example, by recouping energy stores through filial cannibalism, the cannibal can prevent starvation, increase its ability to attract better or more mates, or ensure continuity of care (Rohwer, 1978; Sargent, 1992). While recouping energy presents one explanation for filial cannibalism, both empirical and theoretical studies suggest that the occurrence of offspring cannibalism across species may be driven by a variety of differing selective factors (e.g. Gray, Dill, & McKinnon, 2007; Klug & Bonsall, 2007; Klug, Lindström, & St Mary, 2006; Manica, 2002,

2004). Thus, the evolutionary function and origins of this behaviour remain an active area of study.

Starvation or dwindling energy reserves is one of the most studied driving factors for a parent to cannibalize their own offspring (Manica, 2002). This energy-based hypothesis predicts that cannibalism will increase as parental body condition deteriorates (Rohwer, 1978; Sargent, 1992). The energy recouped through filial cannibalism can be invested into future reproductive attempts, or into the continued care for the remaining offspring (Rohwer, 1978; Sargent, 1992). This hypothesis has been tested empirically in a number of different species. Kvarnemo, Svensson, and Forsgren (1998) showed that supplemental feeding in the laboratory could decrease egg cannibalism in the common goby, *Pomatoschistus microps*. However, supplemental feeding had no effect on either the number of eggs cannibalized in threespine stickleback, *Gasterosteus aculeatus* (Belles-Isles & FitzGerald, 1991), or in the fantail darter, *Etheostoma flabellare* (Lindström & Sargent, 1997). In addition, field studies have also shown that supplemental feeding cannot abolish filial cannibalism in Cortez damselfish, *Stegastes rectifraenum* (Hoelzer, 1992), or a species of Mediterranean blenny, *Aidablennius sphinx* (Kraak, 1996). Therefore, empirical support for the energy-based hypothesis is currently mixed (Klug & Bonsall, 2007; Manica, 2002).

In contrast to filial cannibalism, nonkin cannibalism of another individual's offspring can be viewed as a form of competition. For example, a male can increase his own condition and fitness at the expense of a rival's reproductive success by eating the offspring sired by a competitor (Bertram, 1975; Polis, 1981; Smith & Reay,

* Correspondence: A. P. H. Bose, Aquatic Behavioural Ecology Laboratory, Department of Psychology, Neuroscience, and Behaviour, McMaster University, 1280 Main Street West, Hamilton, ON L8S 4L8, Canada.

E-mail address: boseap@mcmaster.ca (A. P. H. Bose).

1991). For numerous species of fishes, nest take-overs have been documented, wherein a competitive individual displaces a resident for its nest or territory, gaining control over it (Coleman & Jones, 2011). As offspring in a newly acquired nest or territory are typically sired by previous residents, the take-over victor will suffer no direct fitness costs by consuming them (Coleman & Jones, 2011; Sargent, 1989). In the same vein, an association between low paternal certainty and filial cannibalism has been shown in several fish species. For example, in the scissortail sergeant, *Abudefduf sexfasciatus*, the near proximity of potential cuckolders resulted in increased cannibalism of eggs from a caregiving male's brood (Manica, 2004). Male caregivers of both bluegill sunfish, *Lepomis macrochirus* (Neff, 2003a) and threespine stickleback (Frommen, Brendler, & Bakker, 2007) are able to use direct offspring cues to assess their level of paternity over a brood and cannibalize more often when nonkin offspring are present. Even male *Telmatherina sarasinorum*, a species that does not provide parental care, will cannibalize their broods more often if cuckolders are present during spawning (Gray et al., 2007). Still other studies have been unable to show a relationship between paternal certainty and offspring cannibalism (e.g. common goby, *P. microps*: Svensson, Magnhagen, Forsgren, & Kvarnemo, 1998; sand goby, *Pomatoschistus minutus*: Svensson & Kvarnemo, 2007).

Hypotheses for cannibalism as an energy-replenishing tactic and as a competitive tactic are not necessarily mutually exclusive. However, their relative importance within a single study system has not been previously assessed. We tested these two hypotheses in the plainfin midshipman fish, *Porichthys notatus*. This species is a useful model to investigate cannibalism of offspring for a variety of reasons. First, nest-guarding males have a protracted and a presumably energetically taxing parental care period (Craig, Fitzpatrick, Walsh, Wood, & McClelland, 2014; Sisneros, Alderks, Leon, & Sniffen, 2009), which may select for cannibalism as an energy-replenishing strategy. Second, these males compete intensely with each other over nesting sites and access to mates (Cogliati, Balshine, & Neff, 2014; Cogliati, Neff, & Balshine, 2013). In combination with the expression of alternative male tactics, males consequently have surprisingly low levels of paternity in broods that they care for in the wild (on average 52%; Cogliati et al., 2013). This could select for cannibalism as a competitive strategy. Third, male midshipman fish have been documented with conspecific offspring in their digestive tracts (Cogliati, Danukarjanto, et al., 2014; Sisneros et al., 2009), however, the driving factors behind this cannibalism remain unknown.

We examined cannibalism across the long midshipman breeding period, which spans over 3 months (May–July) of care (Cogliati et al., 2013). We explored whether the prevalence of cannibalism changed across the breeding season and whether cannibalism was linked to patterns of energy loss or competition. If caregiving males cannibalize as a result of depleting energy reserves, then we predicted that cannibalism would increase over the breeding season as paternal body condition deteriorates (Sisneros et al., 2009). Alternatively, if cannibalism is a competitive tactic, then we predicted that it would be most frequent early in the season, when male–male competition is most intense (Cogliati et al., 2013). Consequently, the plainfin midshipman system provides the chance to explore cannibalism in a multifaceted way, allowing us to consider both energy-based and competition hypotheses in one species.

METHODS

Study Species

The plainfin midshipman is a marine toadfish (family Batrachoididae) distributed along the west coast of North America, from

California to Alaska (Arora, 1948; Miller & Lea, 1972; Walker & Rosenblatt, 1988). Two alternative male reproductive tactics have been well described in this species (Bass, Horvath, & Brothers, 1996; Brantley & Bass, 1994; Brantley, Wingfield, & Bass, 1993; Cogliati et al., 2013; Lee & Bass, 2004). At the onset of the breeding season, large nest-guarding males (also known as type I) migrate to the intertidal zone, where they excavate a nesting cavity in the soft sediment beneath large rocks (Arora, 1948). As the tides retreat, these guarder males do not leave their nests, even as the small pools of remaining water become hypoxic (Craig et al., 2014). Males can endure these hypoxic conditions through metabolic suppression, a switch to anaerobic pathways (Craig et al., 2014) and a well-adapted system for acid–base regulation (Perry et al., 2010). The guarder males produce an acoustic signal with a specially adapted swim bladder encased in a sonic muscle capable of generating long-duration, low-frequency vibrations (Bass & Marchaterre, 1989; Sisneros & Bass, 2003) to attract gravid females to their nests (Brantley & Bass, 1994; Brantley et al., 1993; Ibara, Penny, Ebeling, van Dykhuizen, & Cailliet, 1983). Typically, the largest males acquire the largest nests and attract the most females (DeMartini, 1988; Fitzpatrick et al., n.d.). Females deposit their entire clutch of eggs (typically 150–300 eggs; A. P. H. Bose & K. M. Cogliati, personal observations; DeMartini, 1988), in a monolayer on the underside of the rock, which is the roof of the nesting cavity (Arora, 1948). Nest-guarder males care for offspring by cleaning, digging and maintaining the nest, fanning the eggs during high tide, hydrating the eggs during low tide, and defending them against egg predators and male competitors (Arora, 1948). Offspring take approximately 60 days to develop into free-swimming juveniles, but because males often continue attracting females, and care for young of various developmental stages, the care period can be longer than 60 days for males of this species (Cogliati et al., 2013), beginning in late April and continuing until early August (Cogliati et al., 2013; Crane, 1981; DeMartini, 1988).

While guarder males care for offspring and court females, sneaker males (also known as type II males) are also present in the population. These smaller males do not build nests, court or provide parental care. Instead, they attempt to fertilize eggs through stealth and sneaking behaviours, whereby they release their sperm while a guarder male spawns with a female (Brantley & Bass, 1994). Interestingly, guarder type I males are sometimes behaviourally flexible and have been observed to cuckold other guarder males (Cogliati, Balshine, et al., 2014; Cogliati et al., 2013; Lee & Bass, 2004). Presumably, this occurs when these males have no eggs in their own nest. If detected, cuckoldry attempts by type I guarder or type II sneaker males or the mere presence of other males in the nest will decrease the nest-guarding male's certainty of paternity over his brood.

Field Observations

A total of 166 plainfin midshipman nests were located between May and July 2013 in the intertidal zone of Crescent Beach (South Surrey, BC, 49°04'N, 122°88'W), a long rocky shoreline that supports a large population of spawning plainfin midshipman. It is a productive, well-sheltered spawning ground with many large rocks that are used as nesting sites, and large nearby eelgrass beds that likely serve as a nursery habitat for newly hatched juveniles. We sampled nests during three periods over the breeding season (23–26 May, 22–26 June, 19–24 July), which corresponded to the early, mid and late breeding season, respectively.

During each period, we checked nests using a short 2-day protocol (consecutive days) to minimize the likelihood of nests gaining new eggs between sampling days or losing nests from unanticipated factors such as predation. On day 1, we laid out 20 m

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